Prehensile Tail Use in Mantled Howler Monkeys (*Alouatta palliata*) and White-Faced Capuchin Monkeys (*Cebus capucinus*)

Research Thesis

Presented in partial fulfillment of the requirements for graduation *with research distinction* in the undergraduate colleges of The Ohio State University

By

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ABSTRACT

The prehensile tail, present in five platyrrhine genera, has evolved in parallel in *Ateles, Lagothrix, Brachyteles,* and *Alouatta,* comprising the atelines, and *Cebus*. While previous studies have examined the anatomical, morphological, and positional differences of prehensile tails, very few have examined how these tails are used, especially in a comparative study. How are prehensile tails used in both *Cebus capucinus* (White-Faced Capuchin Monkeys) and *Alouatta palliata* (Mantled Howler Monkeys), and do they serve similar ecological roles? Both species were studied at La Suerte Biological Field Station in Costa Rica utilizing the "one-zero" sampling technique according to a behavioral ethogram from July 2-July 11, 2015, collecting a total of 24.96 hours of data. *A. palliata* monkeys were found to utilize their prehensile tails more than *C. capucinus* during resting behaviors and *C. capucinus* monkeys utilized their prehensile tails more than *A. palliata* during traveling, which supports my predictions. *C. capucinus* utilized prehensile tails more during both foraging and feeding behaviors than *A. palliata*, which also supports my predictions. Although prior studies show varying results, based on my study, it seems that the prehensile tail serves as a mechanism for balance and maintaining stability during locomotion in larger-bodied *A. palliata*. The prehensile tail of *C. capucinus* also serves as a mechanism for maintaining balance during locomotion in an unstable canopy structure, especially during foraging and feeding in terminal branches.

INTRODUCTION

The Importance of Positional Behavior

Research on animal behavior aims at understanding natural principles, both experimentally and in natural habitats. Field studies allow us to associate behaviors with their adaptive context, which can highlight natural selection (Martin and Bateson, 1993). Comparative studies are particularly important for determining adaptations of individual organisms. Each animal species possesses specific requirements, and problems faced by different species may be solved in different ways (Martin and Bateson, 1993).

When studying the behavior of any animal, it is imperative to understand the definition of behavior and to distinguish the different facets that comprise an animal's behavioral repertoire. Recognizing these facets and behavioral definitions allows us to make distinctions between certain behaviors, categorize them, and observe how they influence an animals' overall behavioral tendencies. Rosenblueth et. al. (1943) defined behavior as any change of an entity with respect to its surroundings, noting that the definition of behavior may be too broad to be useful, resulting in classifications or subcategorized behaviors. More recently, Martin and Bateson (1993) defined behavior as the actions and reactions of whole organisms, involving animals interacting and moving with their environment and one another. While these definitions may differ slightly, they both address how behavior involves animals interacting with their environment. This is an important idea to keep in mind when considering natural selection and adaptation, as behavioral observations may reveal the full functions and evolutionary histories of certain adaptations.

Positional behavior is a general category comprised of both locomotor and postural behaviors (Cant, 1992). Locomotor behaviors are those that occur when a primate's body mass is displaced in relation to its physical surroundings (Prost, 1965). Locomotion is defined as the system by which animals move between locations (Strier, 2011). Common locomotor categories include quadrupedal walking, running, brachiation, and vertical clinging and leaping. Postures occur when the positional relations between a primate's physical surroundings and body mass are fairy stable (Prost, 1965). Examples of postures include suspending by one or more appendages, sitting or perching on hindlimbs, and laying on the ground or a substrate. Positional behavior is an important area of scientific study because locomotor and postural adaptations allow animals to handle major survival problems (Youlatos and Gasc, 2001). Positional behaviors do not provide singular solutions for one general problem, but rather they solve a variety of problems. For example, canopy-dwellers use positional behaviors as a means to deal with certain properties of habitat structure, predation and prey behaviors. Therefore, observing positional behavior under natural conditions is critical for understanding the functional significance of a particular animal's morphology (Cant, 1992).

Problem-Solving Morphological Adaptations

Over the past 55 million years, primates have evolved important morphological adaptations that deal with the problems of balance and support in the arboreal context. Grasping hands and feet and a divergent hallux evolved early in primates. Several authors have attributed these initial changes as mechanisms to

facilitate food exploitation on flexible supports (Garber and Rehg, 1999). Two traits unique to major platyrrhine clades, digital claws and prehensile tails, are adaptive locomotory features (Rosenberger, 2011). Claws and small body size allow callitrichines to exploit vertical tree trunks (Rosenberger, 1992), which is essential for their feeding and vertical clinging method of locomotion. Another adaptation found in some platyrrhines is the prehensile tail. By definition, a prehensile tail is a tail capable of grasping substrates or objects (Strier, 2011). This modified tail provides support during travel and assistance during feeding behaviors in select platyrrhine species (Covey, 2005; Mittermeier, 1978; Fleagle and Mittermeier, 1980; Cant, 1986; Lemelin, 1995; Garber and Rehg, 1999).

An Overview of Prehensile Tails

A prehensile tail is a specialized structure that acts as a fifth limb, allowing an animal to suspend its full body mass without aid from other limbs (Covey, 2005; Garber and Rehg, 1999; Bezanson, 2012). Prehensile tails may also be used in conjunction with one or more limbs (Covey, 2005).

Prehensile tails have evolved independently in six orders of mammals, two suborders of reptiles, and an order of amphibians. While the function of prehensile tails differs between these taxa, grasping tails are generally used for support or locomotive purposes. For example, across fruit-eating (frugivorous), leaf-eating (folivorous), and omnivorous arboreal species like opossums, kinkajous, and porcupines, prehensile tails are used as support during feeding on branch tips or locations that are difficult to reach. They are also used during locomotion, such as on

unstable supports or during descent. For arboreal ant-feeders, prehensile tails are used as a means to free the forelimbs so they can rip into insect nests. Prehensile tails of snakes are used during locomotion, for support, and as an anchor while the body strikes at or circumscribes a prey (Emmons and Gentry, 1983). The prehensile tail in primates is used for added security during rest, to improve foraging behaviors by facilitating suspensory postures, and as an aid during locomotion. In primates, the prehensile tail is employed during locomotion, maintains balance during rest, and improves foraging in terminal branches via suspensory postures (Russak, 2005; Youlatos, 1999).

The Evolution of Prehensile Tails

Prehensile tails evolved independently in various taxa. Is there a single adaptive explanation for prehensile tails across these taxa, or are there different adaptive explanations for different lineages? Drawing on behavioral, ecological, and morphological data, several hypotheses have been offered to address questions about the evolution of prehensile tails. Since the focus of this paper lies within the primate lineage, the hypotheses discussed will address primate prehensile tails.

There are five primate genera that have prehensile tails: *Alouatta, Ateles, Lagothrix, Brachyteles,* and *Cebus*. Four of these genera comprise the atelines; *Cebus* is a non-ateline platyrrhine. Prehensility in platyrrhines is thought to have evolved twice, occurring once in the atelines and once in parallel in *Cebus* (Rosenberger, 1983). Because of the stark differences in *Cebus* and ateline behavior and ecology, it is possible that the parallel evolution of prehensile tails in these taxa occurred due

to different selective pressures (Organ et. al., 2011). Support for this concept is seen in a study done by Organ et. al. (2011), who examined mechanoreceptivity in prehensile tailed primates. Mechanoreception is discriminative touch, including sensations like pressure, tension, stretch, and vibration. The data suggest that while slow-adapting touch sensitivity is important during postural behaviors, rapid-adapting sensitivity of ateline tails may have evolved in response to different selective pressures associated with fine touch, such as during locomotion. Tail bracing behaviors that occur in conjunction with hindlimb suspension or assistance may have contributed to the selective pressure moving towards more sturdy tails capable of prehension, especially among the atelines and *Cebus* (Organ et. al., 2011).

There have been many studies of prehensile tail use in platyrrhines. These studies have identified a number of common themes as well as disagreement concerning which hypothesis is most likely regarding prehensile tail evolution. In all platyrrhines with prehensile tails, the tail is used primarily during feeding behaviors and as a means of providing additional support during travel (Schmitt et. al., 2005; Covey, 2005; Mittermeier, 1978; Fleagle and Mittermeier, 1980; Cant 1986; Lemelin, 1995; Garber and Rehg, 1999). Several hypotheses addressing the evolution of prehensile tails have been proposed (Covey, 2005). The evolution of prehensile tails has often been attributed to maneuvering within fragile forest structure (Covey, 2005; Emmons and Gentry, 1983). Canopies in Neotropical forests have frequent gaps and fragile flora that make moving about difficult (Emmons and Gentry, 1983). Prehensile tails may have evolved as an adaptation to larger body size (Covey, 2005; Napier, 1967; Grand, 1972), due to the difficulties larger body size poses in fragile

Neotropical canopy structures (Emmons and Gentry, 1983). A prehensile tail may help to alleviate the amount of weight placed on each branch during locomotor or postural behaviors, reducing the risk of breaking branches and falling. Suspensory locomotor and postural behaviors are particularly important for larger arboreal animals, as it is easier for large bodied animals to hang below a branch than to balance on top of it (Fleagle and Mittermeier, 1980). Prehensile tails may have evolved as a mechanism to more effectively exploit a frugivorous diet (Covey, 2005; Cant, 1986) and improve terminal branch feeding (Covey, 2005; Grand, 1972). Fruits are typically located on terminal branches in trees (Covey, 2005; Boinski, 1989) that often become thinner towards the tree edges (Covey, 2005; Grand, 1972). Prehensile tails make it easier for larger bodied individuals to feed on these terminal branches, which therefore selects for suspensory behavior (Covey, 2005; Napier, 1967; Cant, 1992).

The majority of evidence seems to suggest that prehensile tails are used most often in the context of feeding and that the most likely hypothesis is that prehensile tails evolved as a means to better exploit frugivorous diets. Other hypotheses, such as the larger body size hypothesis, factor in to the frugivorous hypothesis, as larger animals may be more limited during feeding on fruits. While these hypotheses apply to both the atelines and *Cebus*, neither is unique to one group or species, making it possible that the evolution of a prehensile tail is due to a combination of the proposed factors (Covey, 2005; Meldrum, 1998).

The Role of Canopy Structure and the Evolution of Prehensile Tails

Lianas and palms are types of flora that comprise portions of Neotropical and Paleotropical forests. Lianas are more frequent in Africa, while palms are more frequent in Neotropical forests. Lianas often intersect with tree crowns, providing pathways for arboreal vertebrates to use so animals can bypass branches that may not be able to support their full body weight. Palms are slippery, highly unstable, and are often surrounded by gaps in flora, resulting in a more disjointed canopy structure (Emmons and Gentry, 1983). Palms are less stable than lianas and are surrounded by more gaps in vegetation, which increase the chances of an animal falling. If Emmons and Gentry (1983) are correct, selection should favor adaptations in those arboreal taxa inhabiting Neotropical forests that reduce the chances of falling, particularly in large-bodied taxa. Prehensile tails are used for moving through the canopy specifically in Neotropical environments (Emmons and Gentry, 1983), which supports the idea that unstable canopy structure created a strong selective pressure for the evolution of a stabilizing mechanism, especially for larger animals. This association between body mass and tail prehensility is also supported by tails of extant Cebidae, where the heaviest genera possess prehensile tails, semi-prehensile tails are present in the medium-weight genus, and the lightest genera have nonprehensile tails (Emmons and Gentry, 1983).

Prehensile Tail Anatomy

Morphological study has revealed several important anatomical differences between prehensile and nonprehensile tails. Prehensile tails have more numerous and smaller vertebrae, which allows for greater flexibility compared to nonprehensile tails (Schmitt et. al., 2005). Prehensile tails have stronger, more rigid caudal vertebrae, more expanded sites of muscle attachment, and better developed lateral tail musculature. Prehensile tails also have more extensive ventral musculature with extrinsic tendons that cross fewer joint segments compared to nonprehensile tails (Organ et. al., 2011).

Ateline and *Cebus* prehensile tails differ in several ways, highlighting their parallel evolution. Atelines have less well-developed extensor compartment musculature, while *Cebus* has well-developed dorsal musculature, as is the case in nonprehensile tails (Organ et. al., 2011). The hairless ventral pad unique to atelines is marked by papillary ridges and flexure lines, making it a "friction pad" that is important for maintaining contact with substrates during grasping (Lemelin, 1995; Organ et. al., 2011). This pad is hypothesized to be more sensitive than other hairless skin, as it may contain a higher density of specialized mechanoreceptors that are sensitive to light touch and can assist in texture perception (Organ et. al., 2011). *Cebus*, like most other extant prehensile tailed mammals, lack a friction pad and possess a completely haired tail (Garber and Rehg, 1999). For this reason, *Cebus* prehensile tails are often considered to be semiprehensile, with the most derived prehensile condition being that found in *Ateles* (Bezanson, 2012). However, a tail is considered to be prehensile if it can bear the full body mass of an individual without

aid from other limbs (Covey, 2005; Garber and Rehg, 1999; Bezanson, 2012). Since *Cebus* prehensile tails can suspend the body mass of an adult without aid, they are considered to be fully prehensile (Bezanson, 2012). Compared to their respective trunk sizes, *Cebus* has a relatively short tail while atelines have a relatively long tail that accounts for a slightly higher percentage of their total body mass (Lemelin, 1995; Organ et. al., 2011). Ateline tails have particular representations in the motor and sensory areas of the neocortex that are absent in *Cebus*, as atelines are known to have relatively expanded caudal sensorimotor cortices of the brain (Lemelin, 1995; Organ et. al., 2011). Some have attributed morphological differences between taxa to their different behaviors involving tail use. For example, *Ateles* regularly use full or hindlimb-assisted tail suspension particularly during locomotion or feeding, while *Cebus* frequently wraps the tail around a substrate during feeding, forming a tripod with its hindlimbs (Organ et. al., 2011).

While the ateline and *Cebus* prehensile tails differ anatomically in a variety of ways, they also share some similarities, particularly when compared to nonprehensile tailed primates. Both have robust, strong caudal vertebrae and well-developed lateral tail musculature (Organ et. al., 2011). The upper tail regions in both are longer compared to nonprehensile tailed primates: *Cebus* has six vertebrae, atelines have seven or eight vertebrae, and nonprehensile tailed primates have four or five vertebrae. A more elongated base of the tail allows for a greater range of extension and flexion in this region (Lemelin, 1995).

This Study

While there are several comparative studies regarding the anatomy of prehensile tailed platyrrhines, it is not clear if atelines and capuchins use their tails in similar ways, nor whether their tails satisfy different ecological roles (Garber and Rehg, 1999). Studies have been carried out at the field site where my research was conducted, La Suerte Biological Field Station, including studies of *C. capucinus* prehensile tail use in 1995 and in 2005 (Garber and Rehg, 1999; Covey, 2005). Comparative studies of prehensile tail use have also been done in both *A. palliata* and *C. capucinus*, such as an ontogenetic study of prehensile tail use (Bezanson, 2012). However, there seems to be little comparative data detailing how *A. palliata* and *C. capucinus* use their prehensile tails relative to one another. Without such information, it is difficult to hypothesize what role the tail serves for each species. Some authors discuss how a species uses its prehensile tail for predominantly one activity (Covey, 2005; Mittermeier, 1978; Fleagle and Mittermeier, 1980; Cant, 1986; Lemelin, 1995; Garber and Rehg, 1999). Is this true for all taxa with prehensile tails?

The purpose of this study was to examine prehensile tail use in two species of platyrrhines occupying the same forest habitat. Since both species possess a prehensile tail, yet differ morphologically, my aim was to test whether these anatomical differences might be associated with a difference in ecological roles or behaviors. My hypotheses were based on the general premise that animals differing in size, morphology, and positional behavior should differ in how they solve problems in similar environments (Cant, 1992). In this study, I examined how *A.*

palliata and *C. capucinus* used their prehensile tails in a variety of contexts or maintenance activities. I tested the following hypothesis and associated predictions:

Null hypothesis: There is no difference in prehensile tail use in *A. palliata* and *C. capucinus.* The two species will use their tails in a prehensile manner for the same activities with the same frequencies.

Prediction 1, Travel: During travel, *C. capucinus* will use their tails in a prehensile manner more often than *A. palliata*.

Rationale for Prediction 1: One would expect larger primates to use prehensile tails more when moving simply due to body size, as the branch to body size ratio is much smaller than that of smaller-bodied primates. However, while travel may seem like a function of body weight, I believe that prehensile tail use relies more on locomotor style. The slow arboreal quadrupedal locomotion exhibited by *A. palliata* (Garber and Rehg, 1999) may have evolved as a response to their large body size, overcoming the constraint that large body size imposes. While it is not typical, behavior can act as a way of overcoming the constraints imposed by morphology (McGraw and Daegling, 2012). I also believe that this more careful form of locomotion will not require much prehensile tail use, contributing to a predicted lower frequency of use in *A*. *palliata*. In primates, as body size increases, leaping decreases and climbing increases (Fleagle and Mittermeier, 1980). This means that larger primates are expected to climb and bridge more and leap less compared to smaller primates (Bezanson, 2009). While bridging can involve the use of a prehensile tail, I believe that it will be employed less frequently than the tail during leaping. *C. capucinus*, being of smaller body size, will make 'riskier' movements, such

as leaping, than larger-bodied *A. palliata* during travel that require more stabilization provided by the assistance of a prehensile tail.

Prediction 2, Rest: During resting periods, *A. palliata* will use their tails in a prehensile manner more often than *C. capucinus.*

Rationale for Prediction 2: Due to its greater body weight, I believe *A. palliata* will use its tail in a prehensile manner during rest more than *C. capucinus*. Ateline weights range from 5 to 12 kilograms. *Cebus* weights range from 2 to 3.5 kilograms (Garber and Rehg, 1999). This difference in body size likely contributes to the need for a stabilizing mechanism, as the branch to body size ratio in larger animals is much smaller than that of smaller-bodied primates. Smaller supports are also more likely to deform under the body weight of larger individuals (Bezanson, 2012). The increased security a prehensile tail provides during rest reduces the animal's risk of falling. It is imperative to avoid falling in the canopy, particularly for larger animals. Larger animals are less likely to survive falls from a great height (Fleagle and Mittermeier, 1980).

Prediction 3, Feed and Forage: During feeding and foraging, *C. capucinus* will use their tails in a prehensile manner more often than *A. palliata*.

Rationale for Prediction 3: Based on body size alone, larger-bodied *A. palliata* would be expected to use the tail in a prehensile manner more often than *C. capucinus* during feeding and foraging, as branches are more likely to collapse under the body weight of large individuals (Bezanson, 2012). However, I believe that diet and food distribution are more significant factors contributing to prehensile tail use during foraging and feeding in the two species. *A. palliata* are folivorous while *C.*

capucinus are omnivorous (Bezanson, 2012). *C. capucinus*'s omnivorous diet involves food sources that require manipulation or extraction with the hands (Garber and Rehg, 1999). To manipulate or extract food, *C. capucinus* must have the hands free and the prehensile can provide stability during these hands-free postures by anchoring the body to a support or substrate. *C. capucinus* also uses the prehensile tail as an anchor when feeding on unstable terminal branches (Covey, 2005; Janson and Boinski, 1992), where fruits and insects are often found (Covey, 2005; Boinski, 1989). Branches naturally become thinner towards a tree's periphery (Grand, 1972), making a prehensile tail a valuable resource that anchors an individual to stronger supports towards the center of the tree when the monkey reaches for fruit or insects (Covey, 2005; Janson and Boinski, 1992). As a folivore, *A. palliata*'s food source is more abundant and not restricted to terminal branches like that of *C. capucinus*. This means that *A. palliata* can feed on more stable branches compared to *C. capucinus*. Diet and location of food is a more selective factor than body weight in this case; despite its smaller body size, *C. capucinus* is more vulnerable when feeding because its preferred foods are located in the terminal branches.

METHODS

Data were collected at the La Suerte Biological Field Station in northeastern Costa Rica during July 2nd through July 11th, 2015. La Suerte (10°26'N, 83°47'W) is a tropical wet forest including both primary and advanced secondary forests (Bezanson, 2009). Data were collected in both the Big Forest as well as the

surrounding forested areas at the site (primarily the areas between the main field house and the Big Forest entrance) as seen in figure 1 (Garber and Rehg, 1999).

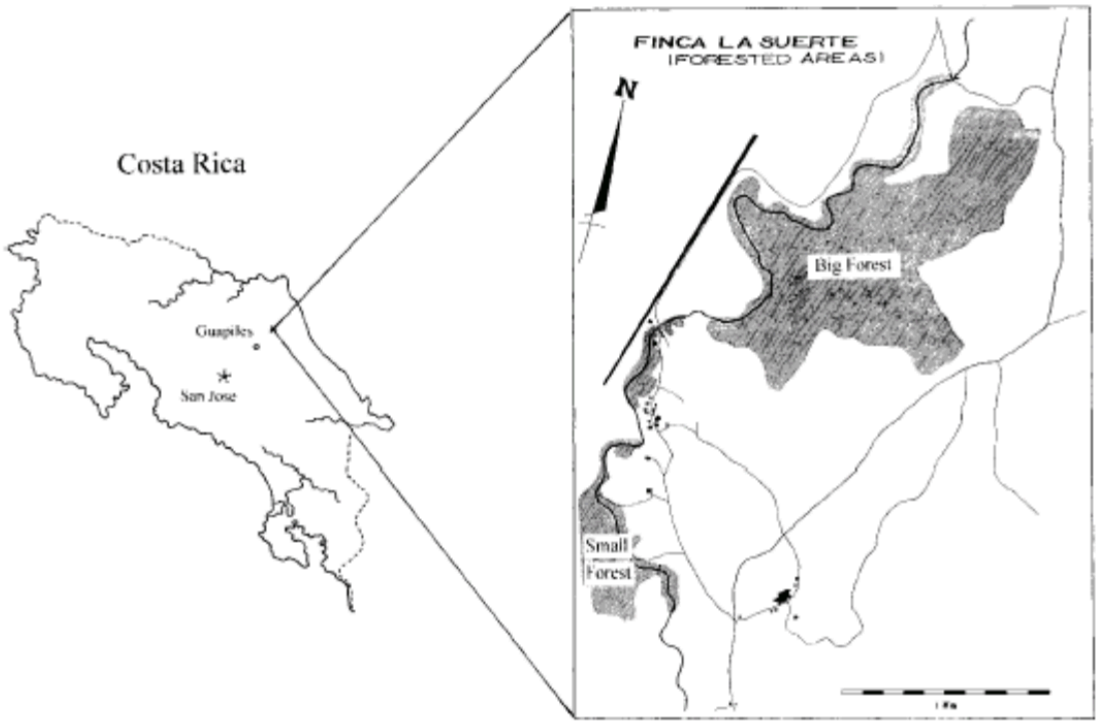

Figure 1- ***Map of La Suerte Biological Field Station***
This map shows the geographical layout of La Suerte Biological Field Station in northeastern Costa Rica, where I conducted my research. Most data collection occurred in the Big Forest and surrounding area to the field house, which lies between the Small and Big Forests (Garber and Rehg, 1999).

Both *A. palliata* and *C. capucinus* were assessed for age-class and sex; however, individual identification was very difficult, so individual identification could not be guaranteed, meaning some individuals may have been sampled more than once. Individuals were sampled as randomly as possible.

I collected a total of 24.98 hours, or 1,499 minutes, of data. 20.68 of these hours (1,241 minutes) were collected on *A. palliata*, 87 total focal samples, and 4.30

hours (258 minutes) were collected on *C. capucinus*, 18 total focal samples. Data were collected using the one-zero sampling technique focusing on one individual at a time. Each focal sample period was 15 minutes long and data were collected at one-minute intervals within these sample windows. Shorter sampling intervals were used in order to properly collect data on specific individuals, while still being able to sample as much of a group as possible. Also, a shorter sampling window was used to account for the differing activity levels of the two species. This sampling technique involves denoting a one (1), affirmative, or a zero (0), negative, indicating whether or not a monkey being sampled has performed this behavior in the time interval. The behaviors observed were categorized using an ethogram, which states the categorical classifications of each behavior. Some categories can occur within the same sampling interval, resulting in overlap of categories within the results.

This study focused only on behaviors in which the tail was used in a prehensile manner, either wrapped around the body of the individual, another animal, or a substrate or object. The grip or wrap need not have been tight or weight bearing. Tail use was assessed based on the level of curvature or activity of the caudal vertebrae; particularly, if the ends of the tail were visibly wrapped or grasping or curled around something, the tail was considered to be in use. Ethogram behavioral categories were created under this general definition of tail use, each category involving the use of the tail in a prehensile way. Each category is as follows:

Rest: stationary behavior, typically in a stable posture, such as a seated position or lying down on a substrate. Eyes may be open or closed.

Travel: when the animal moves more than one or two body lengths in any direction. This can include a variety of strategies, such as arboreal quadrupedalism, jumping, or leaping, and pace may vary.

Forage: animal is searching for or gathering a food source. Animal may be moving or stationary while using hands or feet to sift through/collect a food source. May include quick motions such as lunging out for an insect or fruit.

Feed: eating, chewing, tasting and rejecting, or manipulating a food item. Animal is typically stationary but may be moving and eating simultaneously.

Social: occurs when an animal interacts with one or more individuals in an intraspecific or interspecific manner. Can be in a variety of ways, such as playful behavior, tactile behaviors such as allo-grooming, aggression between individuals, mating or copulatory behaviors, resting while touching other individuals, and infant carrying or nursing.

Other: this category includes behaviors that do not fit in other maintenance categories. These behaviors may be event, or rare, behaviors, that are aside from daily activities or behaviors that seem out of the ordinary. This category can include behaviors such as urine-washing, urinating or defecating, self-grooming, and anointing behaviors when primates rub certain plant items on their bodies. To clarify, self-grooming occurs if the tail is used to groom the body or fur direction, which typically results in the tail wrapping around the body.

Statistical analysis could not be performed on my data set due to my general sampling protocol, small sample sizes and disparity in size between samples of each

species. Given the limitations of statistical analysis, my discussions are based on comparisons of percentages. A legitimate sampling regimen that lends itself to statistical analysis and significance may very well contrast or disprove my results.

RESULTS

The two species utilized all behaviors within the ethogram, but with different frequencies. *A. palliata* used their tail in a prehensile manner most frequently during rest, followed by "other", travel, feed, forage, and social behaviors, as seen in figure 2.

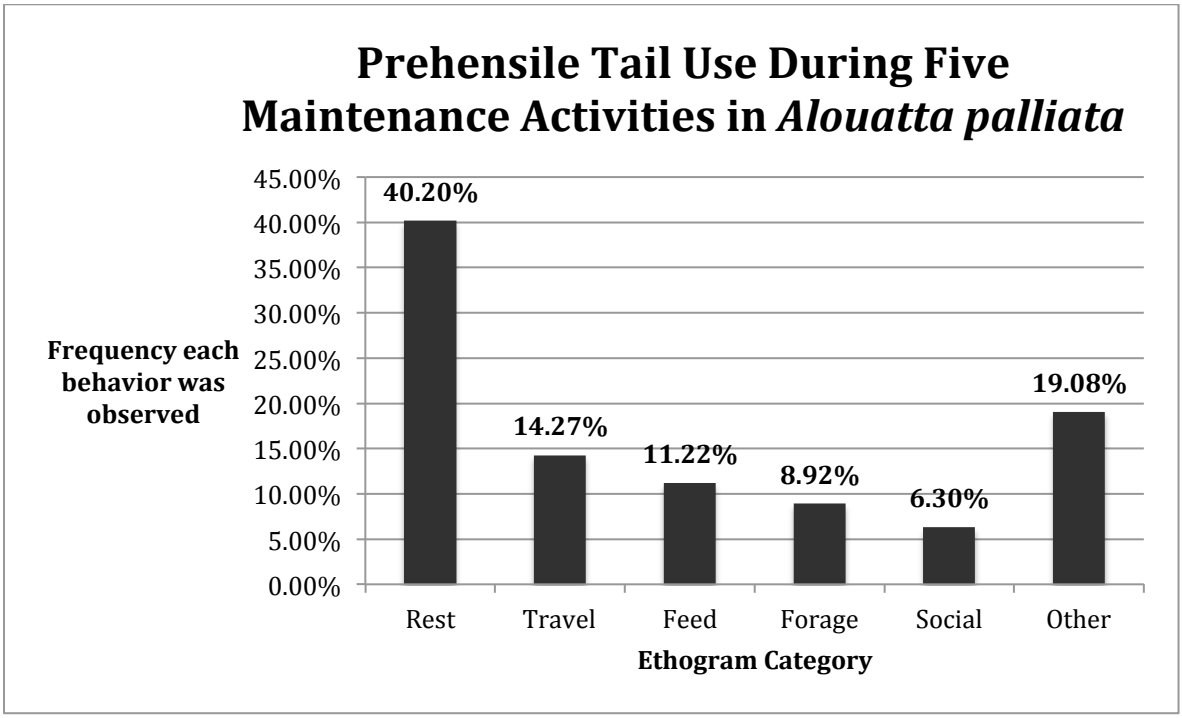

Figure 2- ***Prehensile Tail Use During Five Maintenance Activities in Alouatta palliata***
The frequency that the prehensile tail was used during five maintenance activities in *A. palliata* (n=2557). Rest is the most prominently used behavior, followed by "other", travel, feed, forage, and social behaviors.

C. capucinus used their tail in a prehensile way most frequently during travel, followed by feed, rest, forage, social, and "other" behaviors, as seen in figure 3.

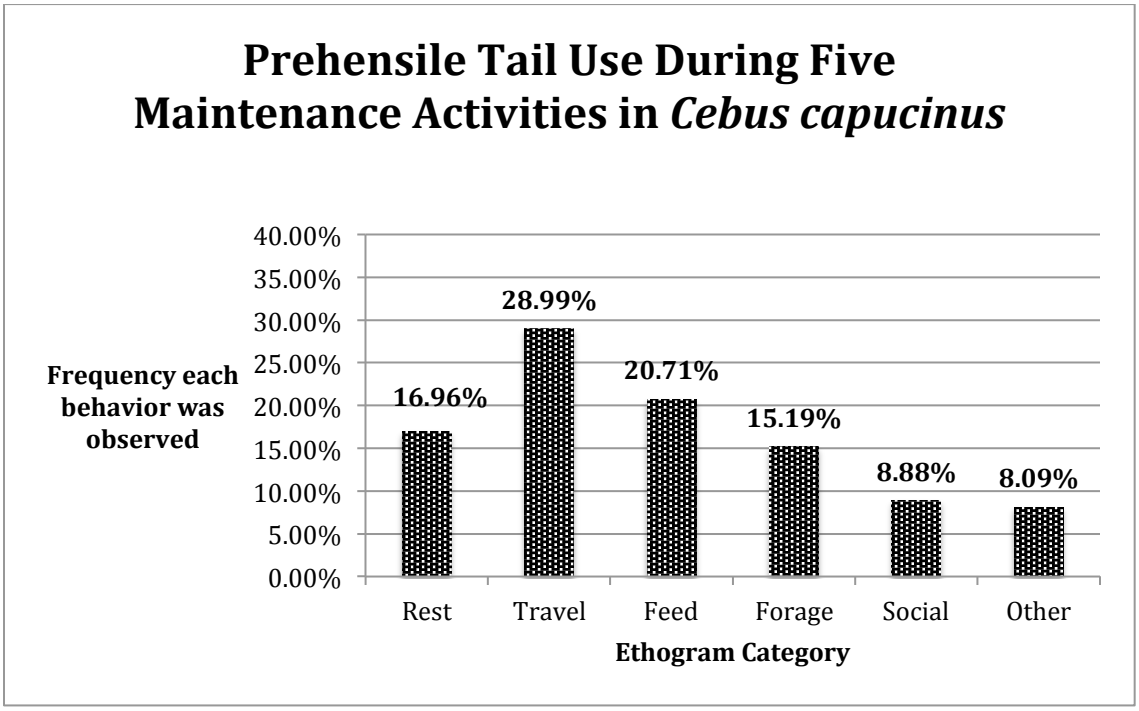

Figure 3-*Prehensile Tail Use During Five Maintenance Activities in Cebus Capucinus*
The frequency that the prehensile tail was used during five maintenance activities in *C. capucinus* (n=507). Travel is the most prominently used category, followed by feed, rest, forage, social, and "other" behaviors.

Continuing to examine figures 2 (*A. palliata*) and 3 (*C. capucinus*), *A. palliata* used its prehensile tail during rest behavior the most and social behavior the least, while *C. capucinus* used its prehensile tail during travel behavior the most and "other" behavior the least. Despite the great disparity in total observation time, *C. capucinus* used its prehensile tail during each behavior more than *A. palliata* except for rest behavior and "other" behavior, as seen in figure 4.

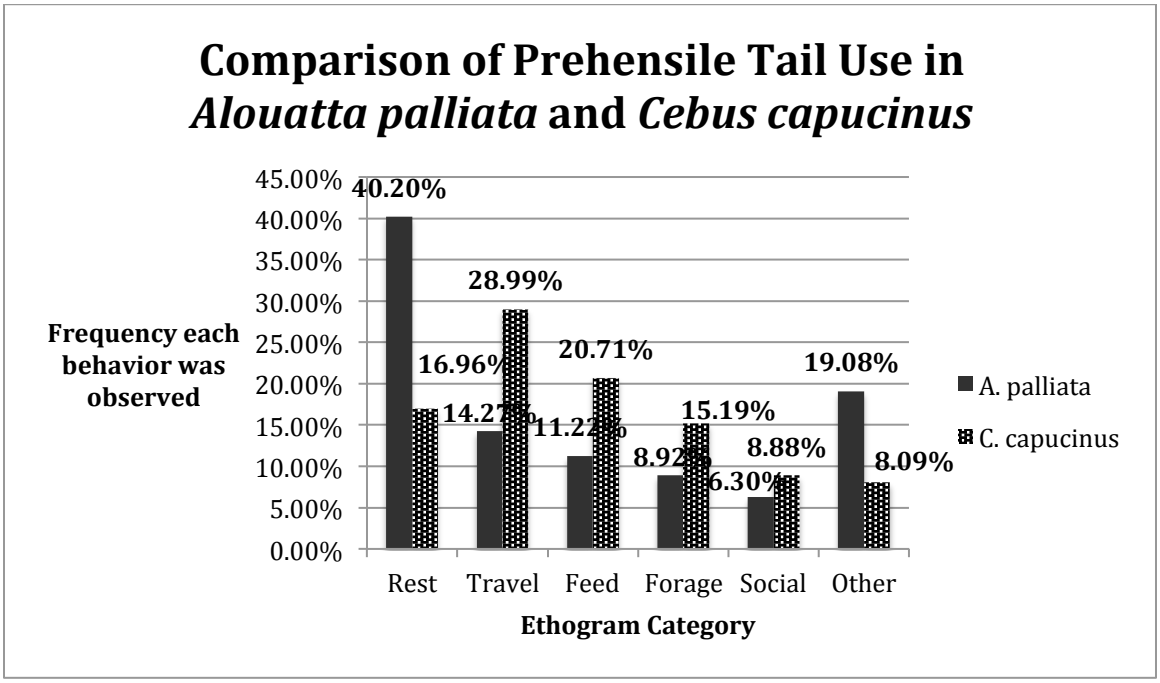

Figure 4- ***Comparison of prehensile tail use in Alouatta palliata and Cebus capucinus***
Comparing prehensile tail use in *A. palliata* (n=2557), displayed as solid, and *C. capucinus* (n=507), displayed as patterned. *A. palliata* used rest and "other" behaviors more frequently than *C. capucinus*, while *C. capucinus* used travel, feed, forage, and social behaviors more than *A. palliata.*

While age and sex differences were not a focus of this project, some basic data were collected and examined for the purpose of identifying possible general age and sex trends. Among *A. palliata*, adults tended to use their tails in a prehensile way more during rest and "other" behaviors, while sub-adults used the tail in a prehensile way more during travel, forage, feed, and social behaviors, shown in figure 5.

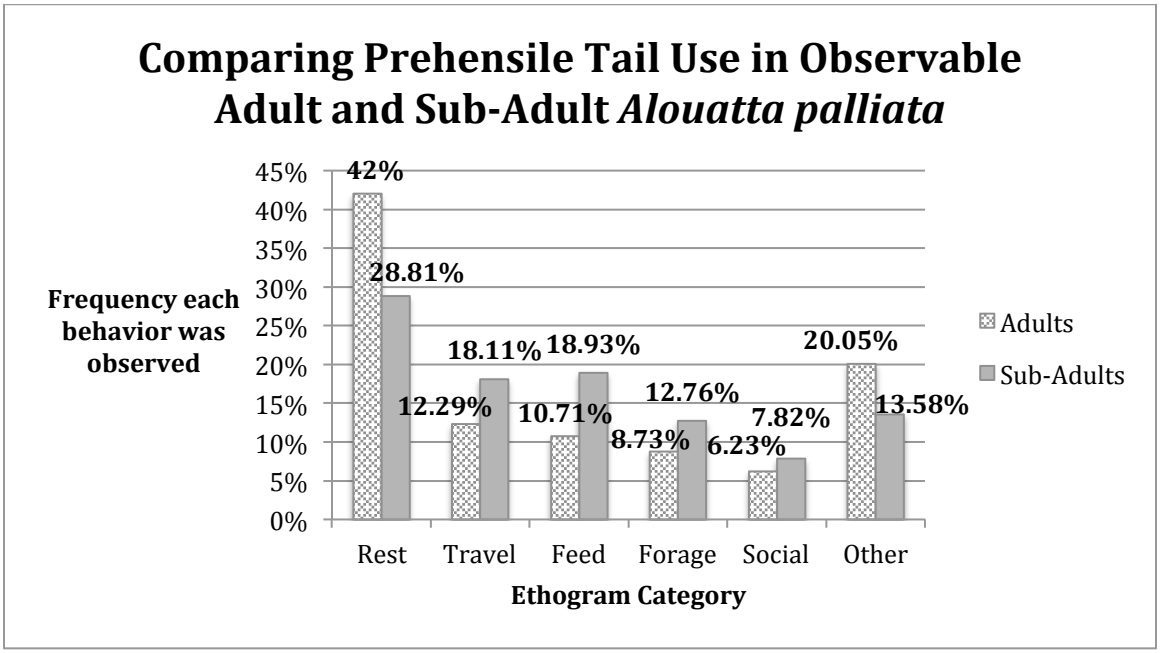

Figure 5- ***Comparing prehensile tail use in observable adult and sub-adult in Alouatta palliata***
Comparing prehensile tail use in observable adult and sub-adult *A. palliata* individuals. It was possible to identify age-class in all individuals sampled, with 80 adults (n=2279) and 7 sub-adults (n=243). Adults tended to use the tail in a prehensile way more during rest and "other" behaviors, while sub-adults used the travel, feed, forage, and social behaviors more frequently.

A. palliata females used their tails in a prehensile fashion more than males during all behaviors except rest and "other", as seen in figure 6.

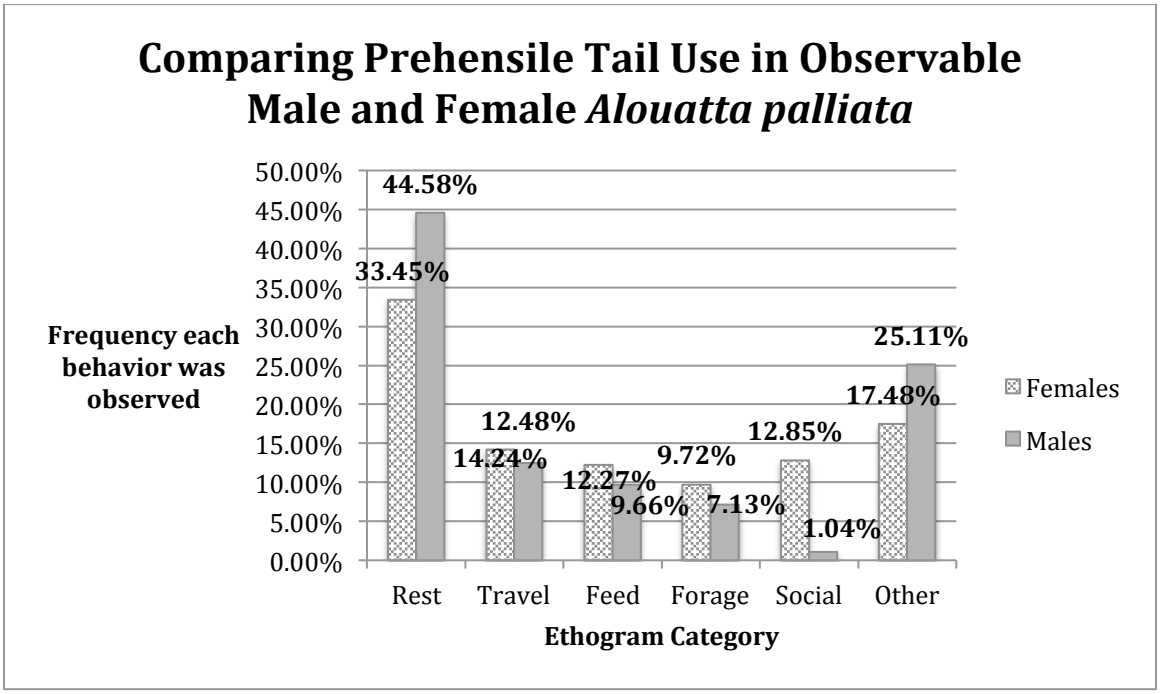

Figure 6- ***Comparing prehensile tail use in observable male and female Alouatta palliata***
Comparing prehensile tail use in observable male and female adult *A. palliata* individuals. Sex was relatively easy to identify in individual samples, but not possible for all samples, with 25 male (n=673) and 25 female (n=864) samples. Females tended to use the tail in a prehensile way more during social, travel, feed, and forage behaviors. Males tended to use the tail in a prehensile way more frequently during rest and "other" behaviors.

C. capucinus adults used each behavior more than sub-adults except for feeding and foraging, as seen in figure 7.

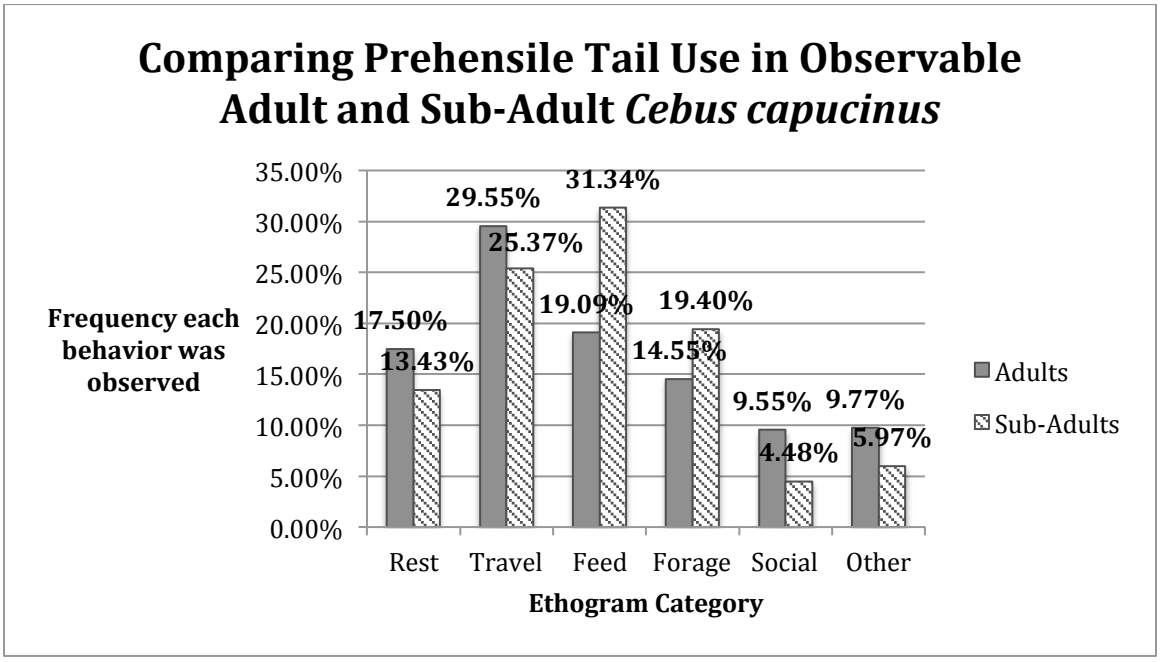

Figure 7- ***Comparing Prehensile Tail Use in Observable Adult and Sub-Adult Cebus Capucinus***

The chart above displays behavioral profiles of prehensile tail use for both adult and sub-adult *C. capucinus* individuals. Age-class identification proved to be difficult in *C. capucinus*, resulting in only 16 identified adults (n=440) and 2 identified sub-adults (n=67). Adults tended to use the tail in a prehensile way more during rest, travel, other, social, and forage behaviors. Sub-adults tended to use the tail in a prehensile way more than adults during feeding, but only by a small margin.

C. capucinus males tended to use their tails in a prehensile manner more than females during travel, feeding, and foraging, and females used rest, social and "other" behaviors more than males, shown in figure 8.

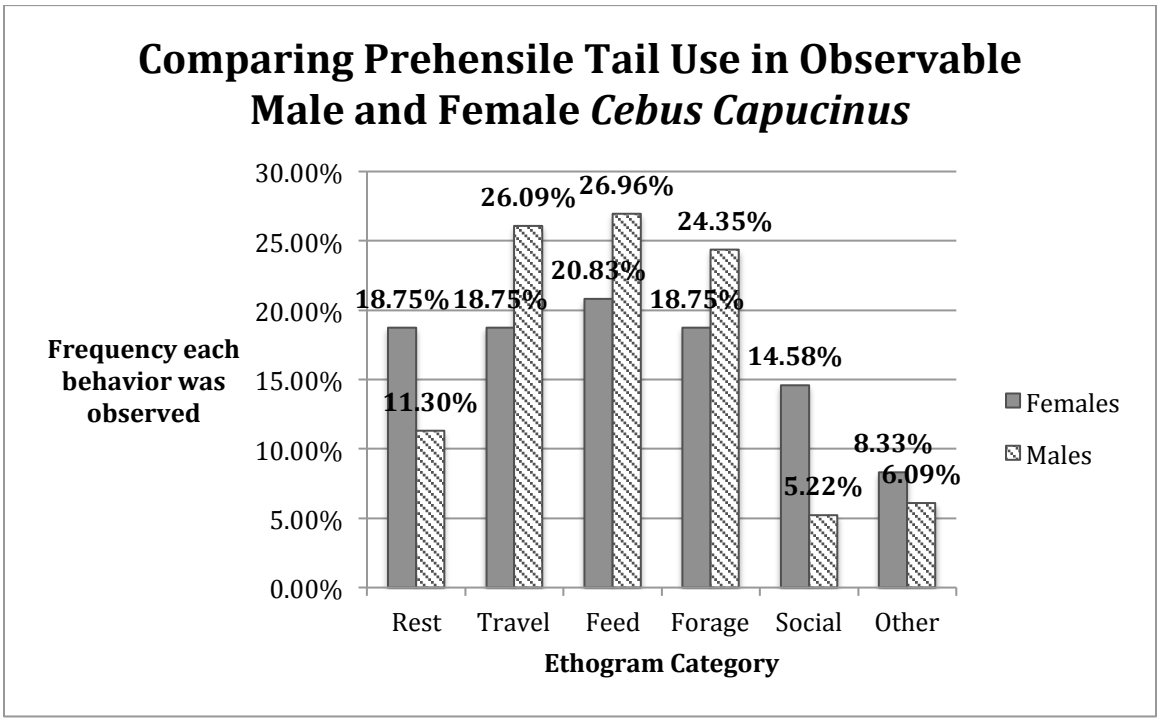

Figure 8- ***Comparing Prehensile Tail Use in Observable Male and Female Cebus Capucinus***
The chart above displays behavioral profiles of prehensile tail use for both male and female *C. capucinus* individuals. Sex proved to be extremely difficult to identify in *C. capucinus*, resulting in only 1 female (n=48) and 4 male samples (n=115). Males tended to use the tail in a prehensile way more than females during travel, feed, and forage behaviors. Females tended to use the tail in a prehensile way more during rest, social and other behaviors compared to males.

Several additional observations are worth mentioning. Overall, *C. capucinus* seemed to use their tails in a prehensile manner less frequently than *A. palliata.* Generally, *A.* palliata tended to use their prehensile tail in a weight bearing or fully suspensory manner more frequently than *C. capucinus*.

DISCUSSION

My null hypothesis that *A. palliata* and *C. capucinus* would show no difference in frequency of prehensile tail use was not supported by my data: *A. palliata* and *C. capucinus* used their tails in a prehensile way at different frequencies for different behaviors, as seen in table 1.

Null Hypothesis	Predictions	Supported by data?
There is no difference in prehensile tail use in *A. palliata* and *C. capucinus.* The two species will use their tails in a prehensile manner for the same activities with the same frequencies.		No
	During travel, *C. capucinus* will use their tails in a prehensile way more often than *A. palliata*	Yes
	During resting periods, *A. palliata* will use their tails in a prehensile way more often than *C. capucinus*	Yes
	During feeding and foraging, *C. capucinus* will use their tails in a prehensile way more often than *A. palliata*	Yes

Table 1-*Hypothesis and Predictions Relative to Collected Data*
The above table provides a summary of my hypothesis and predictions according to my data. My null hypothesis was not supported by my data, meaning that the two species used their tails in a prehensile manner for different behaviors and in different frequencies. My predictions were all supported by my data.

Differences in my results of prehensile tail use of *A. palliata* and *C. capucinus* may be attributed to both behavioral and morphological differences between the two species.

C. capucinus tended to use the tail in a prehensile fashion more frequently than *A. palliata* during travel, supporting my first prediction. I observed that *C. capucinus*, in addition to quadrupedal walking or running, would often jump, leap, or throw

themselves from branch to branch or tree to tree in an exaggerated way. In a previous study on *C. capucinus* at La Suerte, they were observed primarily using quadrupedal walking, climbing and leaping during travel (Garber and Rehg, 1999), which is consistent with my observations. However, in another study of *C. capucinus* at La Suerte, Covey (2005) found that they did not use the tail in a prehensile way much during travel, which contrasts my results. Covey (2005) attributes this to the fact that *C. capucinus* spend most of their time in the lower canopy, which has safer supports and pathways. I believe my results show a higher frequency of prehensile tail use during travel due to the number of leaps by *C. capucinus*. I hypothesize that exaggerated bounds are taken during travel by *C. capucinus* due to their lighter body weight and smaller body size, since smaller primates are expected to leap more compared to larger primates (Bezanson, 2009; Fleagle and Mittermeier, 1980). The exaggerated moves of *C. capucinus* are riskier and require greater stabilization; a prehensile tail can assist with landing and balance. This is likely the main cause of high frequency of tail use during travel behaviors in my study.

Typically, howler monkeys are described as slow arboreal quadrupeds that also employ climbing and bridging postures frequently during travel (Garber and Rehg, 1999). I believe their careful quadrupedal locomotor style evolved as a way of stabilizing their large body during travel. While bridging postures may require the use of a prehensile tail, they were not observed frequently. Slow quadrupedal movements, which occurred more frequently than bridging, may not necessarily require extra assistance from a prehensile tail, although how the prehensile tail was used during specific locomotor styles was not directly studied.

A. palliata used the tail in a prehensile way more frequently during rest than did *C. capucinus*. Looking at only activity budgets, one might attribute this to the high frequencies of rest in *A. palliata*, which can reach 80% of activity budgets in some studies (Estrada et. al., 1999; Kowalewski et. al., 2015). However, I attribute the high frequency of prehensile tail use during rest in my study to differences in body weight between *A. palliata* and *C. capucinus*. Atelines weigh anywhere from 2-9 kilograms more than Cebus (Garber and Rehg, 1999). The branch to body size ratio is much smaller in *A. palliata* than in *C. capucinus*, due to *A. palliata*'s larger body size. This contributes to a more frequent use of the prehensile tail in *A. palliata* because a larger body on top of a small support likely needs a way of stabilizing during above-branch behaviors, such as resting. Smaller supports are also more likely to deform under the body weight of larger animals (Bezanson, 2012; Cant, 1992). In this case, prehensile tails act as a fail-safe mechanism in case branches break under *A. palliata*'s larger body weight. The prehensile tail helps prevent larger arboreal animals such as *A. palliata* from falling. Larger animals are particularly vulnerable as they are less likely to survive a fall from great heights compared to smaller animals (Fleagle and Mittermeier, 1980). While data were not collected on substrate use, I observed *A. palliata* resting on small branches, often high in trees and in precarious positions (figure 9), while *C.* capucinus would rest on larger supports such as crooks of trees or the centers of bamboo clusters. Having more stable supports to rest on likely contributed to the low frequency of prehensile tail use during rest in *C. capucinus*.

Figure 9-*Photo of A. palliata resting*
Two *A. palliata* individuals resting. I took this photo at La Suerte Biological Field Station in the Big Forest.

C. capucinus used the tail in a prehensile manner more than *A. palliata* during feeding and foraging. This difference can be attributed to variation in diet and food distribution rather than body weight. If only body weight is considered, *A. palliata* would be expected to use the tail in a prehensile way more frequently than *C. capucinus* during feeding and foraging, since branches are more likely to deform or break under the body weight of larger animals (Bezanson, 2012). However, my results contradict this idea, making it an unlikely explanation for prehensile tail use during feeding and foraging.

Rather, prehensile tail use during feeding and foraging is primarily determined by food distribution and overall diet. As folivores (Bezanson, 2012), *A. palliata*'s food is more abundant and evenly distributed. As omnivores (Bezanson, 2012), *C. capucinus*'s food is more dispersed and typically clustered on or near terminal branches (Covey, 2005; Boinski, 1989). Branches gradually become thinner towards a tree's periphery (Grand, 1972), which makes feeding and foraging on terminal branches dangerous. A prehensile tail is used as an anchor around stronger supports away from unstable terminal branches so *C. capucinus* can then reach for fruits or insects (Covey, 2005; Janson and Boinski, 1992; Boinski, 1989). As omnivores, *C. capucinus*'s diet also includes foods that require manipulation or extraction with the hands (Garber and Rehg, 1999). Extracting and manipulating food requires the hands to be free, which can be facilitated by use of a prehensile tail. By using the prehensile tail as an anchor for the rest of the body, *C. capucinus* can effectively obtain and eat food items while remaining safely secured to a support.

Although I do not have robust data to confirm this, my impression is that prehensile tail use differed between adults and sub-adults as well as males and females of each species. *A. palliata* adults used their prehensile tails more often than sub-adults during rest and "other" behaviors. *C. capucinus* sub-adults used their prehensile tails more often during feeding and foraging behaviors compared to adults. I believe that sub-adults used their prehensile tails more often than adults during various active behaviors because they are less experienced than adults and are learning how to safely navigate the canopy, acquire and manipulate food properly, and interact in a group setting. *A. palliata* females tended to use the tail in a prehensile way more during social, travel, feed, and forage behaviors by small margins except for during social behaviors. The higher frequency of female prehensile tail use during social behaviors is likely attributed to the higher frequency of interactions with offspring compared to males. *C. capucinus* males used their prehensile tails more often than females during travel, feeding, and foraging, which could be due to their larger body size compared to females (Bezanson, 2012).

It is important to emphasize again that I cannot assert with confidence any conclusions regarding age and sex differences in *A. palliata* and *C. capucinus* prehensile tail use. The sample sizes for my observations of age and sex are too small to make any generalizations about either species. Identifying age and sex was not always possible in all samples, resulting in highly varied sample sizes for each comparison. Identification proved to be particularly difficult in *C. capucinus*. While I attempt to justify my results and explain their implications, I cannot make any

statistical declarations or confident interpretations that apply to each species as a whole.

I observed that out of their total behavioral repertoire, *C. capucinus* seemed to use their tails in a prehensile manner less frequently than *A. palliata* overall. This observation is consistent with other published research (Lemelin, 1995; Organ, 2010), supporting the hypothesis that increased tail use would be observed in larger bodied *A. palliata* compared to *C. capucinus* (Bezanson, 2006, 2009, 2012; Bergeson, 1996; Cant, 1986). This is most likely due to the greater need to maintain stability in larger individuals, as the branch to body size ratio is smaller compared to that of smaller primates.

My observation that *A. palliata* tended to use their prehensile tail in a weight bearing or fully suspensory manner more frequently than *C. capucinus* also agrees with Lemelin (1995) and Organ (2010). The hairless "friction pad" of *A. palliata* may be responsible for this observation, as it is important for maintaining contact with substrates during grasping (Lemelin, 1995; Organ et. al., 2011). This pad is hypothesized to be more sensitive than other hairless skin, as it may contain a higher density of specialized mechanoreceptors that are sensitive to light touch and can assist in texture perception (Organ et. al., 2011). Sensing texture of a substrate may increase the confidence a primate has to fully suspend its body weight, as it can differentiate between slippery and dry surfaces. *Cebus* lack a friction pad and possess a completely haired tail (Garber and Rehg, 1999), which may hinder *C. capucinus'*s ability to sense the texture of a support or substrate and confidently assess its stability. However, other studies suggest that tail suspensory postures are

more common in *C. capucinus*, (Bezanson, 2012; Bezanson, 2009; Garber and Rehg, 1999; Youlatos, 1999), so my observations and associated explanations may not be definitive.

Implications and Future Work

At La Suerte, *A. palliata* use their tails in a prehensile way most often during rest behaviors, followed by "other", travel, feed, and forage behaviors. The high frequency of prehensile tail use during rest and travel behaviors compared to feed and forage behaviors suggest that the prehensile tail's function is primarily to maintain stability in *A. palliata*. *C. capucinus* use their tails in a prehensile manner the most during travel behaviors, followed by feed, rest, and forage behaviors. The frequency of prehensile tail use during these behaviors suggests that the prehensile tail's function in *C. capucinus* is to maintain stability and facilitate safe travel, while still aiding in food acquisition and consumption. My results imply that the prehensile tails of *A. palliata* and *C. capucinus* do not serve the same ecological role, although they do serve similar functions but in different ways. While various hypotheses have been proposed regarding the evolution of prehensile tails, my study suggests that locomotor stability and safe navigation of unstable canopy structures may be a primary function, as opposed to evolving as a foraging or hunting apparatus, such as in kinkajous, opossums, and snakes (Emmons and Gentry, 1983). However, with traits that evolve in parallel, such as the prehensile tail, we cannot discount the idea that the original evolutionary function of a trait may not be the same function it serves in extant individuals. The prehensile tail may be an example of an exaptation, a trait that now serves a different purpose from its

original evolutionary function. Meldrum (1998) suggests that prehensile tails initially evolved as a postural adaptation and later evolved as a locomotor adaptation in spider monkeys, implying that the platyrrhine prehensile tail is an example of an exaptation. Due to my limited time frame for data collection and small sample sizes, further research should be done to better examine prehensile tails in platyrrhines to produce more conclusive results. By examining other prehensile-tailed members of the atelines and *Cebus,* a more detailed analysis can be done regarding the ecological role of the prehensile tail. These analyses can then be used to assess the relationship between extant functions of the prehensile tail and their evolutionary origins, revealing how this trait evolved in parallel within some platyrrhines.

SUMMARY AND CONCLUSIONS

1. In *A. palliata*, use of the tail in a prehensile way occurred most often during rest (40.20%), followed by "other" (19.08%), travel (14.27%), feeding (11.22%), foraging (8.92%), and social behaviors (6.30%).
2. In *C. capucinus*, use of the tail in a prehensile manner occurred most often during travel (28.99%), followed by feeding (20.71%), resting (16.96%), foraging (15.19%), social (8.88%) and "other" behaviors (8.09%).
3. *A. palliata* used their prehensile tails more frequently than *C. capucinus* during resting behaviors, while *C. capucinus* used their prehensile tails more frequently than *A. palliata* during traveling, feeding, and foraging. These data support my predictions.

4. My results suggest that the prehensile tail of *A. palliata* serves as a mechanism for maintaining stability and facilitating safe navigation of canopy structures. My results also suggest that the prehensile tail of *C. capucinus* serves as a mechanism for maintaining stability during locomotion, with an emphasis on safely and effectively acquiring and consuming food sources. These results suggest that prehensile tails in the atelines and *Cebus* may have evolved as a way of maintaining stability and facilitating safe postural behaviors. However, the current functions of prehensile tails may not be the same as their original adaptive functions, suggesting that this trait could be an exaptation. While my results and ideas proposed in this study may not explain how prehensile tails evolved in platyrrhines, they provide a framework for understanding the possible evolutionary pathways for this trait. Further research on other members of the atelines and *Cebus*, including expanded, sample sizes would allow me to more confidently analyze my results and compare them to other published works.

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